

A Lower Cretaceous palynoflora from Carregueira (Lusitanian Basin, westernmost Iberia): taxonomic, stratigraphic and palaeoenvironmental implications

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ABSTRACT

Here we describe a new Lower Cretaceous palynoflora from the Lusitanian Basin, located in the westernmost sector of the Iberian Peninsula. The spore-pollen assemblage was extracted from samples collected in the Carregueira clay pit complex, located near the village of Juncal, western Portugal, from sedimentary deposits belonging to the Figueira da Foz Formation. A rich and well-preserved palynoflora, typical of non-marine fluvial environments, was recovered. Fifty-eight species and morphological groups of palynomorphs in 43 genera were recognized. The palynoflora is dominated by fern spores and conifer pollen. Angiosperm pollen is scarce and mainly represented by *Afropollis*, *Clavatipollenites*, *Stellatopollis* and *Senectotetradites*. Comparisons with described marine sections in Portugal suggest that the fossil horizon is lower Albian, corresponding to a hiatus between Zone I and Zone II in the Potomac Group of the eastern USA. The same beds contain a mesofossil flora dominated by angiosperm seeds, fruits and flowers. A similar contrast in the relative abundance of angiosperm mesofossils and pollen is seen at other Portuguese localities but is not evident in the Potomac Group. The palynoflora and the sedimentological data suggest deposition in wet lowland environments in a moderately humid regional setting.

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1. Introduction

Angiosperms and angiosperm-dominated ecosystems are in geological terms young and follow a long series of changes in the plant cover on Earth since colonization of the land by spore-bearing plants in the Early Palaeozoic. Angiosperm diversification through the Cretaceous is of utmost importance because it caused radical changes in terrestrial ecosystems. Earlier Mesozoic ecosystems with floras dominated by ferns, conifers, cycads, Bennettitales and other

groups of extinct plants were largely replaced by angiosperm-dominated vegetation during the mid-Cretaceous (Lidgard and Crane, 1988; Wing and Boucher, 1998; Friis et al., 2011).

The Cretaceous rocks of the Lusitanian Basin (western Portugal) comprise an extensive sedimentary sequence with abundant and well-preserved plant fossils at different stratigraphic levels. These strata contain exceptional mesofossil floras including flowers, fruits, seeds and other reproductive structures (Friis et al., 1999, 2000, 2006, 2010, 2011, 2015, 2018, 2019; von Balthazar et al., 2005; Pedersen et al., 2007; Mendes et al., 2011, 2014a, b; Mendes and Friis, 2018), which have contributed to understanding of the systematic diversity and evolutionary diversification of angiosperms and associated plants, in many cases using phylogenetic methods (Friis et al., 2009, 2015; Doyle and Endress, 2014, 2018). Other plant fossils such as leaves and twigs have provided general evidence on vegetational composition (Heer, 1881; Saporta, 1894; Romariz, 1946;

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Teixeira, 1945, 1947, 1948, 1950, 1952), while palynological assemblages including pollen, spores, and in some cases dinoflagellates (Groot and Groot, 1962; Hasenboehler, 1981; Pais and Reyre, 1981; Médus, 1982; Berthou and Leereveld, 1990; Trincão, 1990; Heimhofer et al., 2005, 2007; Horikx et al., 2014, 2016, 2017) have mostly addressed stratigraphic issues. These palynofloras have yielded significant data that complement inferences from leaf and mesofossil floras and can provide important clues for the reconstruction of ancient ecosystems (Schrank, 2010; Mendes et al., 2011, 2014a, 2017, 2018, 2019; Mendes and Friis, 2018; Tanrikulu et al., 2018).

The geographic distribution of plants is largely controlled by temperature and precipitation regimes, which make them reliable palaeoclimatic and palaeoecological indicators. Pollen and spores are among the most important proxies due to their abundance in the fossil record, their broad sampling of the regional vegetation, and the direct relationship between vegetation composition and environmental changes. Furthermore, palynomorphs together with other climatic proxies, i.e., sedimentology, can contribute to better understanding of the changing climate in the Lusitanian Basin during the Cretaceous (Mendes et al., 2011, 2014a, 2018; Heimhofer et al., 2012).

Here we describe a new Lower Cretaceous palynoflora from near the base of the Figueira da Foz Formation in westernmost Iberia and compare it with palynofloral sequences elsewhere in Portugal, in England, and in North America. The sample locality is the Carregueira opencast clay pit complex, located near the village of Juncal in the central-western mainland Portugal. Based on the palynological and sedimentological data, we aim to assess the past regional vegetational composition and palaeoclimatic conditions prevailing during the deposition of the Figueira da Foz Formation.

2. Geological setting

The present study deals with Cretaceous material from the Lusitanian Basin in the westernmost sector of the Iberian Peninsula (Wilson et al., 1989), between the towns of Nazaré and Leiria (central-western mainland Portugal) (Fig. 1A). In this area (Fig. 1B), the Cretaceous is represented by two major sequence-stratigraphic units, UBS4 – uppermost Aptian to lower Campanian – and UBS5 – upper Campanian to lower Eocene (Cunha, 1992; Cunha and Pena dos Reis, 1995; Dinis et al., 2008) (Fig. 2). To the south of the study area, in the vicinity of Torres Vedras, the 1:50 000 geological map of the Portuguese Geological Survey (Carta Geológica de Portugal, Folha 26-B, Alcobaça; França and Zbyszewski, 1963) referred to the Lower Cretaceous as the “Grés com vegetais fósseis de Torres Vedras e Cercal” (Sandstones with fossil plants of Torres Vedras and Cercal). Subsequently this unit has been thoroughly investigated by several authors (Rey, 1972, 1993; Dinis et al., 2002; Rey et al., 2003), and part of it is now assigned to the Figueira da Foz Formation (Dinis et al., 2008).

In the study area, the Figueira da Foz Formation is about 260–280 m thick and comprises mainly fluvial to nearshore siliclastic deposits. This unit passes upwards and laterally (toward the SW) into the brackish and marine carbonates (limestones and marls) of the Costa de Arnes Formation (middle Cenomanian to lower Turonian; Berthou, 1984; Callapez, 1998). Palaeocurrents measured from the Figueira da Foz Formation in the region indicate a regional fluvial drainage towards WSW (Dinis et al., 2008).

An opencast clay pit complex located ($39^{\circ} 35' 25''$ N; $08^{\circ} 55' 33''$ W) near the village of Juncal was selected for detailed study (Fig. 1). The sampled site is an exposure of around $5 \text{ m} \times 20 \text{ m}$, containing sedimentary deposits ascribed to the Famalicão Member, situated about 30 m above the base of the Figueira da Foz Formation (Fig. 2;

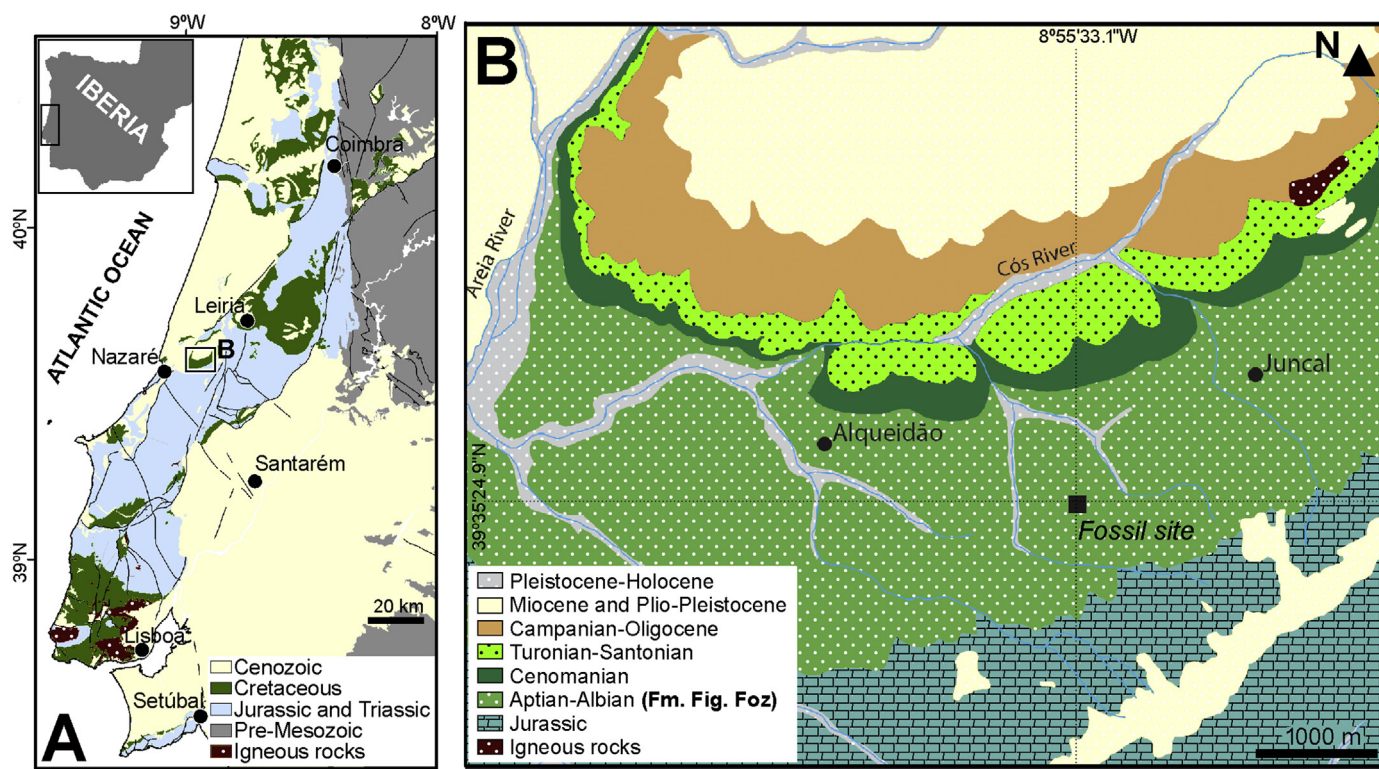


Fig. 1. Geological setting of the investigated site. A. Sketch map of the Lusitanian Basin in central-western mainland Portugal (westernmost Iberian Peninsula) (adapted from Oliveira et al., 1992). B. Detailed geological map showing the location of the Carregueira clay pit complex (black square), where the specimens were collected (cartography adapted from the Carta Geológica de Portugal, 1:50,000, Folha 26-B).

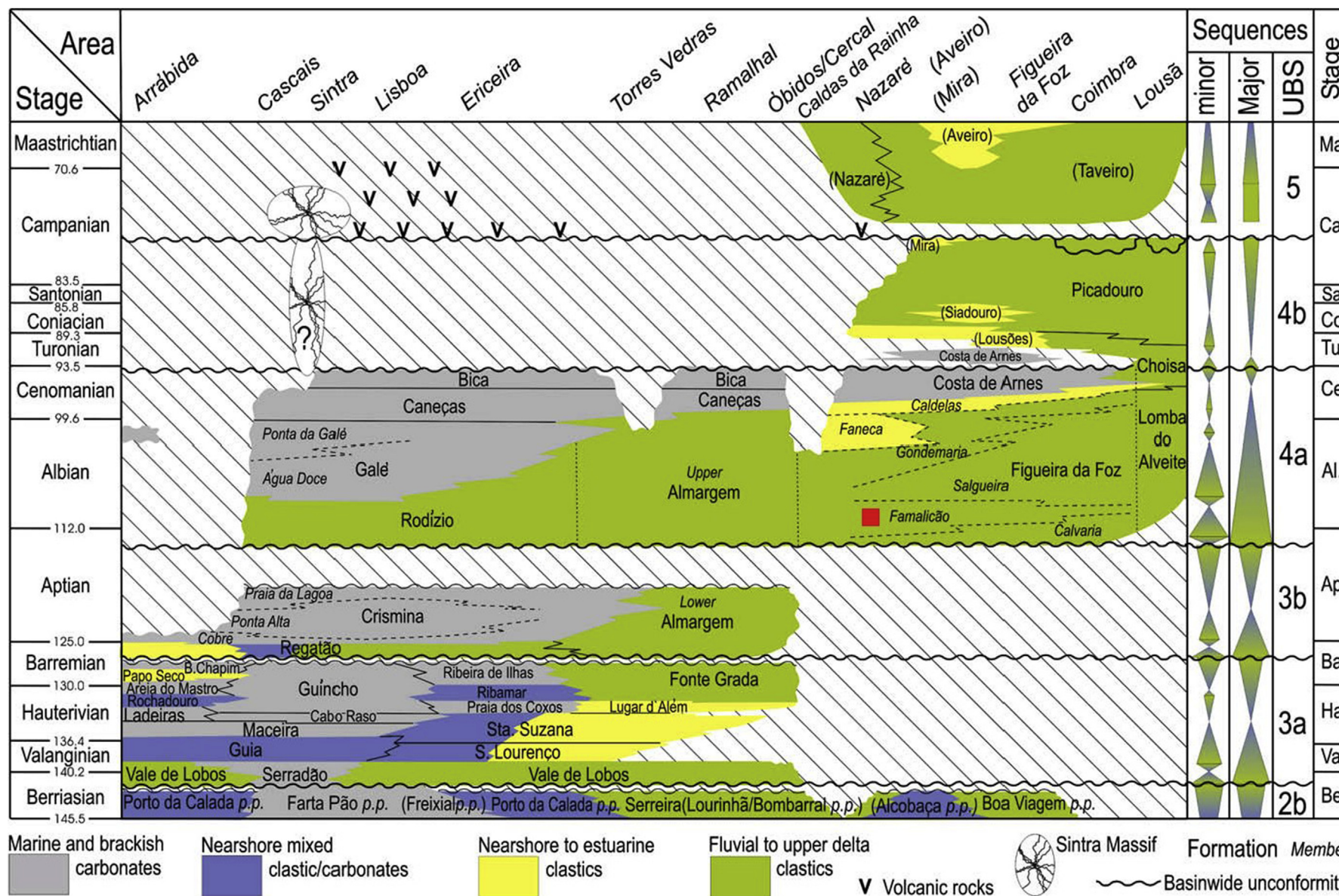


Fig. 2. Synthetic lithostratigraphic chart of the Cretaceous of the western Portuguese margin (Dinis et al., 2008). UBS: unconformity bounded sequences after Cunha and Pena dos Reis (1995). The red square indicates the geographical and stratigraphical position of the studied site. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Dinis et al., 2008). In the study area, the Famalicão Member has been considered upper Aptian or lower Albian (Teixeira, 1950; Friis et al., 1999, 2010) or upper lower Albian (Heimhofer et al., 2005, 2007) based on macrofossils, palynology, and sequence-stratigraphic considerations. This stratigraphic assignment is compatible with the framework of Atlantic rifting events for West Iberia, namely a post-rift transgression associated with the onset of seafloor spreading to the northwest of the Iberian Peninsula in the late Aptian (Rey, 2006; Dinis et al., 2002, 2008).

3. Material and methods

Rock samples were collected by M.M. Mendes and P.P. Cunha at the Carregueira opencast clay pit complex. Although only the basal part of the sampled site provided plant remains, the palaeontology and sedimentology of the Cretaceous succession of the Carregueira clay pit complex were studied in detail to improve our understanding of the local stratigraphy and sedimentology. Fieldwork included stratigraphic logging and sedimentological characterization of the deposits in order to obtain data on the depositional facies, including rock colour, texture, clast lithology, fossil content, bedding and depositional architecture.

At the studied stratigraphic section, six samples (B.Carr 1 to B.Carr 6) were collected for sedimentological characterization (Fig. 3). Grain-size distributions of fine-grained deposits were obtained by laser diffraction using a Coulter LS 230 granulometer. The

clay mineralogy was determined by X-ray diffraction (XRD) using an Aeris instrument (Malvern PanAlytical) with Cu K-alpha radiation. XRD analyses were performed on oriented aggregates (<2 µm), separated by centrifugation according to Stokes' law, both on air-dried slides (2–30° 2θ) and after solvation with ethylene glycol and heating at 550 °C (2–15° 2θ). Semi-quantitative estimations of mineral proportions were based on the areas of their characteristic reflections after the application of correction factors (Moore and Reynolds, 1997; Kahle et al., 2002). Grain-size and mineralogical analyses were carried out in the laboratories of the Earth Sciences Department of University of Coimbra.

Twenty samples were processed following standard palynological techniques (Traverse, 2007). Palynomorphs were extracted from rock samples of ca. 50 g using concentrated HCl (10%) and HF (40%). The organic residue was then oxidized in concentrated HNO₃ (69%) followed by repeated washing with distilled water over a 125 µm mesh nylon sieve until neutral in order to remove larger coal fragments. All the material passing through the sieve was concentrated by centrifuging and then retained in distilled water in small glass vials.

For light microscopic (LM) studies, five glycerine jelly microscope slides were prepared from each sample and sealed with nail varnish. LM pictures were taken with a Nikon Coolpix 5400 digital camera on a Nikon Eclipse E600 microscope using ×60 and ×100 objectives. Counts of specimens from each of the six productive samples were made in order to assess the quantitative composition of the flora.

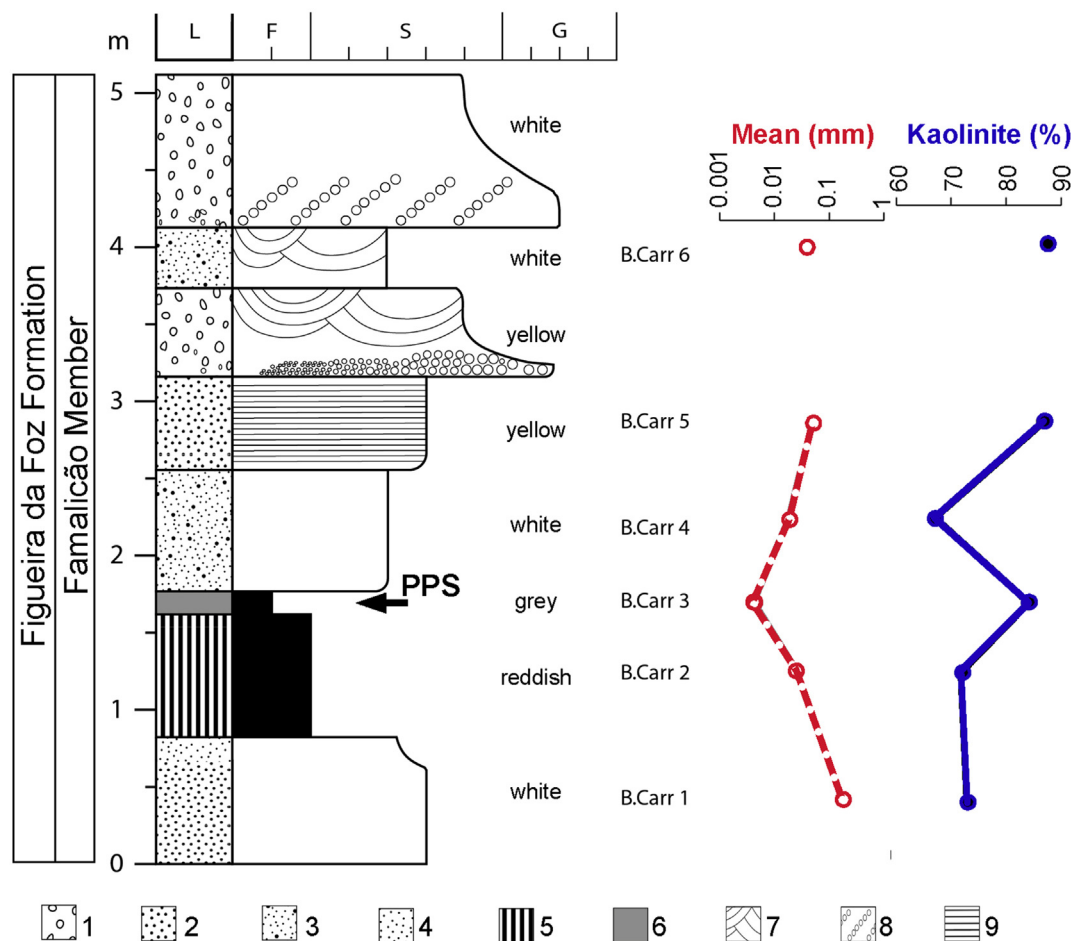


Fig. 3. Stratigraphic column obtained for the Carregueira exposure. Mean grain-size of collected samples and kaolinite proportion in the clay fractions are also indicated. Legend: L – Lithological column; F – Fines; S – Sands; G – Gravels; B.Carr 1 to 6 – rock samples; 1 – gravel; 2 – very coarse pebbly sand; 3 – coarse sand; 4 – medium sand; 5 – silt; 6 – clay; 7 – trough cross lamination; 8 – planar lamination; 9 – horizontal lamination. (PPS) – Palynologically productive samples.

LM slides used for the study are housed in the Geological Museum of Lisbon, Portugal, under the acronym JUN-CAR.

The study horizon also contains a small mesofossil flora currently being studied by E.M Friis and coworkers. This flora is dominated by angiosperm fruits, seeds, and flowers, which consist mainly of taxa that are well known from other Portuguese localities: e.g., *Anacostia* (Friis et al., 1997), *Canrightiopsis* (Friis et al., 2015), *Saportanthus* (Friis et al., 2017), and seeds representing Nymphaeales or Austrobaileales (Mendes and Friis, 2018).

4. Results

4.1. Sedimentary deposits

The studied succession (~5 m thick; Fig. 3) represents entirely continental deposits typical of a fluvial environment. The rocks consist predominantly of white and yellowish sandstones, generally displaying trough and planar cross laminations or horizontal lamination. Coarser-grained beds tend to show fining-upward gradation, yielding sub-rounded quartz and quartzite gravels (clasts up to ~4 cm in diameter) near their flat or concave-upward bottom surfaces. Intercalated fine-grained deposits consist of a reddish siltstone (~1 m thick) that passes upward to a thin layer of grey mudstone. The grain-size distributions of the sampled deposits are poorly sorted and skewed toward the finer fraction. Clay assemblages are characterized by a predominance of kaolinite with secondary illite and, occasionally, minor amounts of smectite.

In these fluvial deposits, mud layers and mud-drapes record low-energy overbank deposition from suspension in floodplains or small lakes. Renewal of the water energy shortly after the deposition of the fine-grained facies limited bioturbation by plant roots, preventing its complete reworking. Compositional features provide additional information about environmental conditions. Abundant kaolinite is common in wet and warm environments (Chamley, 1989; Velde, 1995), but it may also be associated with post-depositional chemical decomposition of feldspar in porous sandstone beds (Hundert et al., 2006). However, the kaolinite enrichment in fine-grained beds suggests intense weathering in the drainage area instead of a diagenetic origin.

4.2. The palynoflora

Out of the 20 samples collected from the Carregueira section, only six samples were productive, all from the same stratigraphic level, B.Carr 3 (Fig. 3). The palynofloral assemblages from the six samples contain abundant and generally well-preserved miospores together with rare aquatic palynomorphs (Figs. 4–6). Fifty-eight species of palynomorphs (also including two undifferentiated morphological groups) assigned to 43 genera were recognized (Table 1): 30 spore taxa, 20 gymnosperm taxa, five angiosperm taxa and three species of fresh-water algae.

Miospores include spores of bryophytes, lycophytes and pteridophytes (ferns), and pollen grains assigned to gymnosperms and angiosperms (Table 1). Gymnosperm pollen is most abundant, reaching about 48% of the total recovery from the productive samples. Fern spores are frequent and reach nearly the same percentage as gymnosperm pollen (41.0%). Less abundant are bryophyte spores (3.0%) and lycophyte spores (3.0%). Angiosperm pollen reaches just over 2%.

Among the fern spores, representatives of the families Anemiaceae (16.5%), Cyatheaceae/Dicksoniaceae (5.0–7.6%, depending on whether *Cyathidites australis* and *Cyathidites punctatus* belong to this group or to Lygodiaceae) and Lygodiaceae (4.5–7.1%) occur in

the Carregueira palynoflora. Anemiaceae (Schizaeales) are represented by trilete spores with coarse and compact ridges assigned to the genera *Appendicisporites*, *Cicatricosisporites* (Fig. 5J, K), *Costatoperforosporites* (Fig. 5L) and *Plicatella*. *Cicatricosisporites* sp. A (Fig. 5K) and *Cicatricosisporites hallei* (Fig. 5J) are the most abundant species of their genus. Lygodiaceae (also Schizaeales) may be represented by *Ischyosporites* (Fig. 5D, E). Cyatheaceae/Dicksoniaceae are represented by smooth-walled spores assigned to *Cyathidites australis* (Fig. 5G). Verrucate spores identified as *Concavissimisporites informis* (Fig. 5F) and *Cyathidites punctatus* (Fig. 5I) have been compared to both Lygodiaceae and Cyatheaceae/Dicksoniaceae. Relatively common and diverse ornamented pteridophytic spores include the marsileaceous *Crybelosporites pannuceus* (Fig. 4J, K) and specimens of uncertain botanical affinity ascribed to *Patellasporites tavadensis* (Fig. 4H). A few spores assigned to *Cibotiumspora juncta* (Fig. 5H), which may represent Matoniaceae or Gleicheniaceae, were recorded.

Lycophyte spores are represented by *Camarozonosporites insignis* (Fig. 5A, B) and possibly *Densoisporites velatus* (Fig. 4G). Bryophyte spores are rare and represented by *Aequitridites verrucosus* (Fig. 4C), *Triporeletes reticulatus* (Fig. 4D) and *Taurocusporites segmentatus* (Fig. 4E).

Aquatic palynomorphs include two species of Zygnemataceae ascribed to *Ovoidites* (Fig. 4A) and one species of Chlorophyta assigned to *Schizosporis* (Fig. 4B). No marine palynomorphs were observed.

The most common gymnosperm pollen grains in the Carregueira palynoflora are the circumsulcate *Classopollis* (Fig. 6B, C), produced by the extinct conifer family Cheirolepidiaceae (14.0%), and bisaccate pollen grains (Fig. 6G, H), representing Pinaceae and possibly a few Podocarpaceae and seed ferns (9.0%). Other prominent gymnosperm pollen types are *Araucariacites australis* (Fig. 6F) and other types representing Araucariaceae (10.4%), probable Cupressaceae, including *Spheripollenites psilatus* (Fig. 6A), and *Cycadopites follicularis* (Fig. 6E), which may be bennettitalean. Rare polyplicate grains of *Ephedripites* indicate the presence of Gnetales. Furthermore, pseudotricolpate (trisulcate) pollen grains assigned to *Eucommiidites* (Fig. 6D) represent the extinct gymnosperm order Erdtmanithecales.

Angiosperm pollen is rare in the studied samples but is important from a plant evolutionary perspective, as well as for interpretations of the palaeoecology, palaeogeography and stratigraphy. The most common angiosperm pollen are represented by finely reticulate monosulcate grains assigned to *Clavatipollenites hughesii* (Fig. 6J), which has been associated with Chloranthaceae (Friis et al., 2011; Doyle and Endress, 2018). It is most similar to pollen of the extant genus *Ascarina*, but it has been found adhering to the mesofossil *Canrightiopsis* (Friis et al., 2015), which phylogenetic analyses place below *Sarcandra* and *Chloranthus*, and it has been inferred to represent the ancestral pollen type for the family (Friis et al., 2015; Doyle and Endress, 2018). Another monosulcate angiosperm type is *Stellatopollis barghoornii* (Fig. 6I), of unknown affinities, which has distinctive “crotonoid” or “stellate” sculpture consisting of triangular supratelal elements. It was first described from the Potomac Group (Doyle et al., 1975) but is more common in Northern Gondwana (Doyle et al., 1977; Penny, 1986; Ibrahim, 2002). Eudicots are represented by a tetrad of tricolpate grains attributed to *Senectotetradites* (Fig. 6K). Interestingly, coarsely reticulate, spheroidal pollen assigned to *Afropollis* (Fig. 6L), which is abundant in Northern Gondwana but rare elsewhere (Doyle et al., 1982; Villanueva-Amadoz et al., 2011), also occurs in the assemblage. Its affinities are uncertain, since it has been reported in pollen sacs that show no evidence of angiosperm relationships (Friis et al., 1999, 2011; Doyle and Endress, 2010).

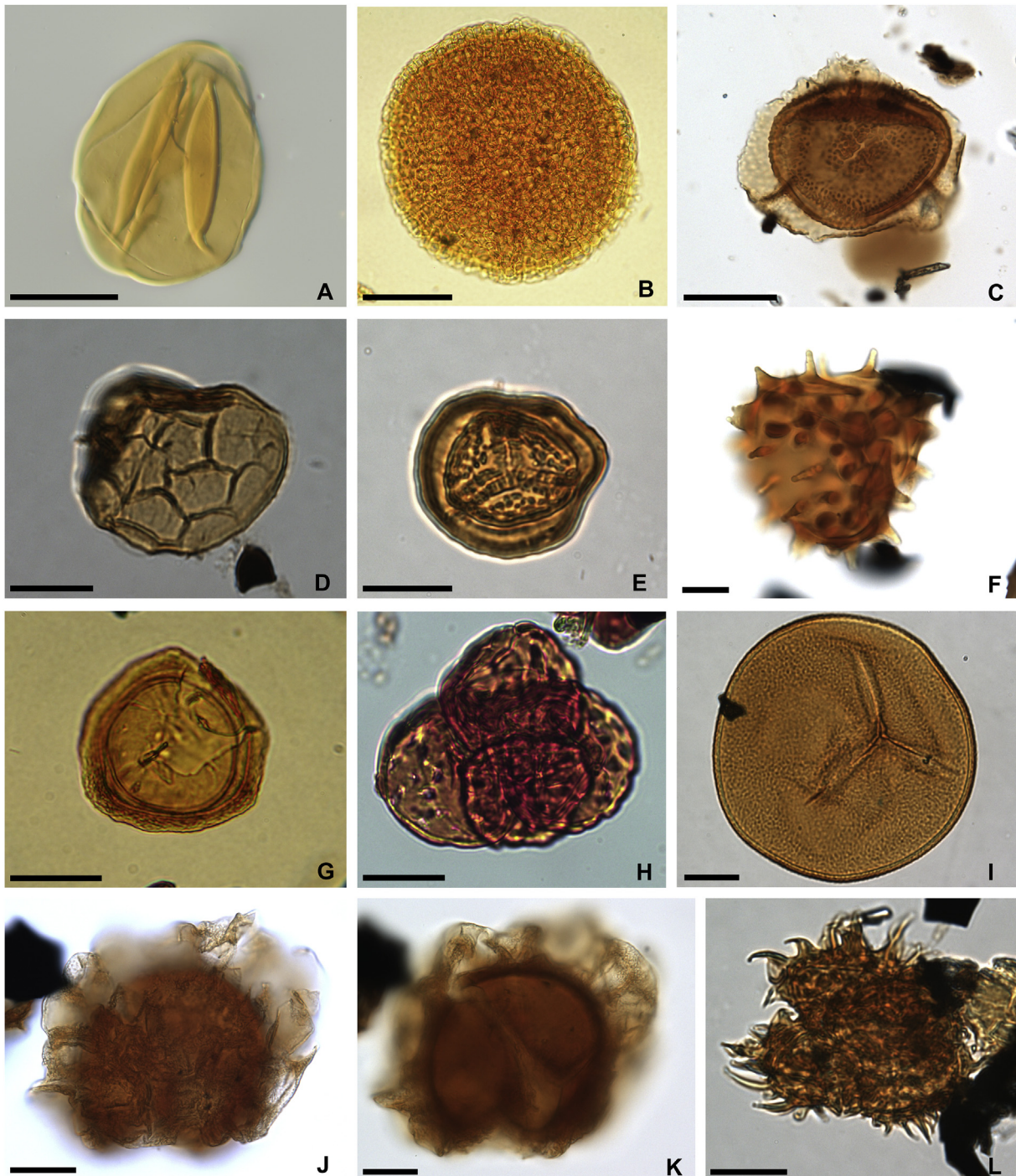


Fig. 4. Transmitted light photomicrographs of some spore types recovered from the Early Cretaceous palynoflora of the Carregueira site. The letters and numbers after each entry are slide references. **A.** *Ovoidites spriggii* (Cookson & Dettmann, 1959) Zippi 1998 (MS.3 JUN-CAR 63; sample Juncal 63). **B.** *Schizosporis reticulatus* Cookson & Dettmann 1959 emend. Pierce 1976 (MS.4 JUN-CAR 63; sample Juncal 63). **C.** *Aequitriradites verrucosus* Cookson & Dettmann 1961 (MS.4 JUN-CAR 63; sample Juncal 63). **D.** *Tripolorletes reticulatus* (Pocock, 1962) Playford 1971 (MS.2 JUN-CAR 100; sample Juncal 100). **E.** *Taurosporites segmentatus* Stover 1962 (MS.3 JUN-CAR 101; sample Juncal 101). **F.** *Apiculatisporis babsae* Brenner 1963 (MS.2 JUN-CAR 102; sample Juncal 102). **G.** *Densoisporites velatus* Weyland & Krieger 1953 emend. Dettmann 1963 (MS.3 JUN-CAR 102; sample Juncal 102). **H.** Tetrad of *Patellasporites tavadensis* Groot & Groot 1962 (MS.3 JUN-CAR 102; sample Juncal 102). **I.** *Todisporites major* Couper 1958 (MS.1 JUN-CAR 103; sample Juncal 103). **J.** *Crybelosporites pannuceus* (Brenner 1963) Srivastava 1977 (distal view) (MS.1 JUN-CAR 103; sample Carregueira 103). **K.** *Crybelosporites pannuceus* (Brenner 1963) Srivastava 1977 (proximal view) (MS.1 JUN-CAR 103; sample Juncal 103). **L.** Tetrad of *Ceratosporites parvus* Brenner 1963 (MS.3 JUN-CAR 103; sample Juncal 103). Scale bars: 20 μ m.

5. Discussion

5.1. Palaeobiogeographic and stratigraphic considerations

As is typical of floras from the upper part of the Lower Cretaceous, the Carregueira palynoflora is dominated by ferns and

gymnosperms but also contains sparse angiosperm pollen. In phytogeographic terms, it belongs to the Southern Laurasia province of Brenner (1976), which extended from middle palaeolatitudes of North America through Europe to East Asia. This province was intermediate between Northern Laurasia (Siberia, Alaska, Canada) and Northern Gondwana (Africa and South

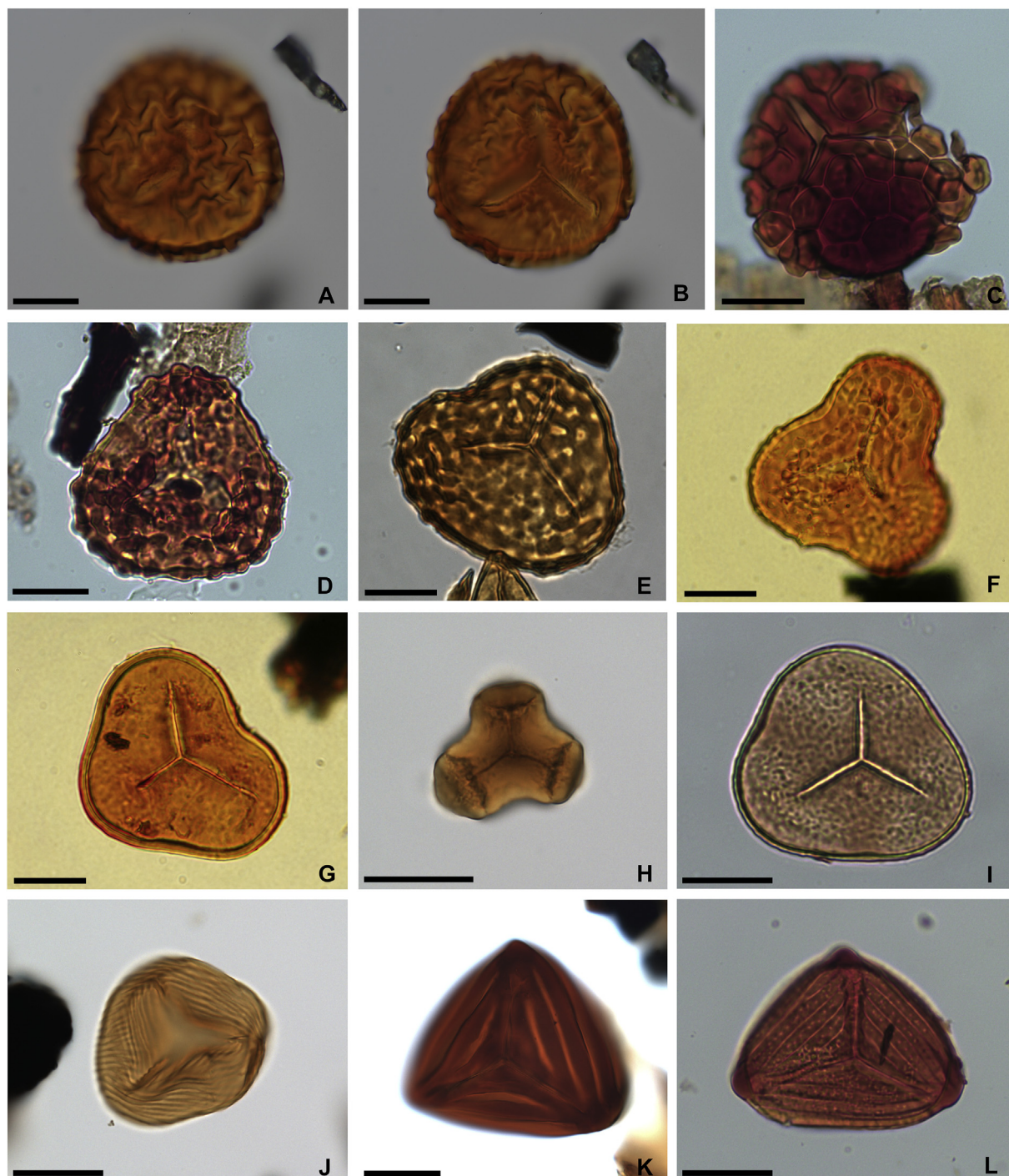


Fig. 5. Transmitted light photomicrographs of some spore types recovered from the Early Cretaceous palynoflora of the Carregueira site. The letters and numbers after each entry are slide references. **A.** *Camarozonosporites insignis* Norris 1967 (distal view) (MS.1 JUN-CAR 101; sample Juncal 101). **B.** *Camarozonosporites insignis* Norris 1967 (proximal view) (MS.1 JUN-CAR 101; sample Juncal 101). **C.** *Gregussosporites orientalis* Juhász & Smirnova 1985 (MS.5 JUN-CAR 101; sample Juncal 101). **D.** *Ischyosporites punctatus* Cookson & Dettmann 1958 (MS.5 JUN-CAR 101; sample Juncal 101). **E.** *Ischyosporites pseudoreticulatus* (Couper, 1958) Döring 1965 (MS.2 JUN-CAR 102; sample Juncal 102). **F.** *Concavissimisporites informis* Döring 1965 (MS.4 JUN-CAR 102; sample Juncal 102). **G.** *Cyathidites australis* Couper 1953 (MS.5 JUN-CAR 102; sample Juncal 102). **H.** *Cibotiumspora juncta* (Kara-Murza, 1956) Zhang 1978 (MS.5 JUN-CAR 102; sample Juncal 102). **I.** *Cyathidites punctatus* (Delcourt & Sprumont, 1955) Delcourt, Dettmann & Hughes 1963 (MS.3 JUN-CAR 103; sample Juncal 103). **J.** *Cicatricosisporites hallei* Delcourt & Sprumont 1955 (MS.4 JUN-CAR 103; sample Juncal 103). **K.** *Cicatricosisporites* sp. A (MS.5 JUN-CAR 103; sample Juncal 103). **L.** *Costatoperforosporites* sp. (MS.5 JUN-CAR 103; sample Juncal 103). Scale bars: 20 μ m.

America, except for their southern extremities). The conifers were a mixture of taxa that were also abundant in Northern Laurasia, namely Pinaceae (with bisaccate pollen) and Cupressaceae (including former Taxodiaceae), and taxa that were dominant in Northern Gondwana, namely Cheirolepidiaceae (*Classopollis*) and

Araucariaceae. Bisaccate pollen was almost entirely absent in Northern Gondwana, but it reappeared in Southern Gondwana (southern South America and Africa, India, Australasia), where was presumably produced by Podocarpaceae. Southern Laurasia is notable for a high diversity of spores, with the striate to coarsely

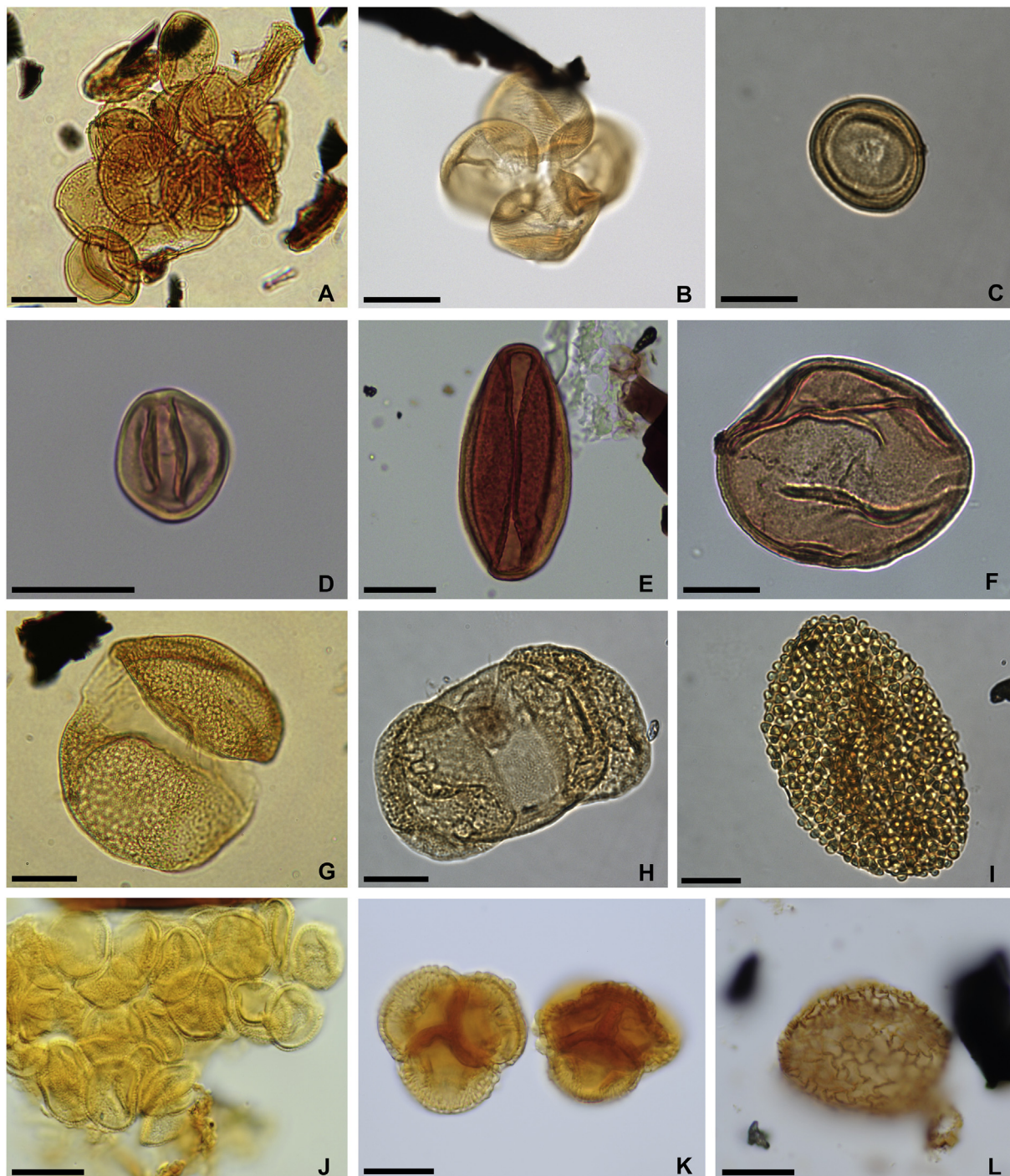


Fig. 6. Transmitted light photomicrographs of some pollen types recovered from the Early Cretaceous palynoflora of the Carregueira site. The letters and numbers after each entry are slide references. **A.** Cluster of *Spheripollenites psilatus* Couper 1958 (MS.4 JUN-CAR 63; sample Juncal 63). **B.** Tetrad of *Classopollis torosus* Burger 1965 (MS.5 JUN-CAR 63; sample Juncal 63). **C.** *Classopollis* sp. (MS.3 JUN-CAR 100; sample Juncal 100). **D.** *Eucommiidites troedssonii* Potonié 1958 (MS.3 JUN-CAR 101; sample Juncal 101). **E.** *Cycadopites follicularis* Wilson & Webster 1946 (MS.5 JUN-CAR 101; sample Juncal 101). **F.** *Araucariacites australis* Cookson 1947 (MS.3 JUN-CAR 102; sample Juncal 102). **G.** *Alisporites rotundus* Rouse 1959 (MS.1 JUN-CAR 100; sample Juncal 100). **H.** *Pinuspollenites* sp. (MS.3 JUN-CAR 102; sample Juncal 102). **I.** *Stellatopollis barghoornii* Doyle 1975 (MS.3 JUN-CAR 63; sample Juncal 63). **J.** Cluster of *Clavatipollenites hughesii* Couper 1958 (MS.2 JUN-CAR 102; sample Juncal 102). **K.** *Senectotetradites* sp. (obligate tetrads) (MS.4 JUN-CAR 102; sample Juncal 102). **L.** *Afropollis* sp. (MS.2 JUN-CAR 103; sample Juncal 103). Scale bars: 20 μ m.

reticulate- verrucate spores of the fern order Schizaeales (Anemiaceae, Lygodiaceae) being especially prominent. By contrast, in Northern Gondwana spores varied from highly subordinate in some regions to abundant but relatively low in diversity in others. The palaeoecological significance of these variations is discussed further below.

Most members of the Carregueira palynological assemblage belong to long-ranging taxa such as *Cyathidites*, *Classopollis*, *Araucariacites*, and *Spheripollenites*. However, features such as the diversity of *Cicatricosisporites* species (Anemiaceae) are indicative of an Early Cretaceous age (Traverse, 2007).

Table 1

Spore and pollen taxa identified in the Carregueira palynoflora, with species listed alphabetically within genera. Absolute numbers (N°) and percentages (%) of taxa are based on combined counts from all six productive samples.

Taxon	N°	%	Botanical affinity
Aquatic palynomorphs			
<i>Ovoidites parvus</i> (Cookson & Dettman, 1959) Nakoman 1966	5	0.3	Zygnemataceae
<i>Ovoidites spriggii</i> (Cookson & Dettmann, 1959) Zippi 1998	11	0.7	Zygnemataceae
<i>Schizosporis reticulatus</i> Cookson & Dettmann 1959 emend. Pierce 1976	14	0.9	Chlorophyta
		0	
Spores			
<i>Acritosporites oculatus</i> (Deák, 1965) Juhász 1979	13	0.8	Pteridophyta (Lygodiaceae)
<i>Aequitriradites verrucosus</i> Cookson & Dettmann 1961	24	1.5	Bryophyta (Hepaticae)
<i>Apiculatisporis babsae</i> Brenner 1963	32	2.0	Lycophyta or Pteridophyta
<i>Appendicisporites tricornitatus</i> Weyland & Greifeld 1953	22	1.3	Pteridophyta (Anemiaceae)
<i>Baculatisporites</i> sp.	12	0.7	Pteridophyta (Osmundaceae)
<i>Camarozonosporites insignis</i> Norris 1967	13	0.8	Lycophyta (Lycopodiaceae)
<i>Ceratosporites parvus</i> Brenner 1963	14	0.9	Lycophyta (?Selaginellaceae)
<i>Cicatricosisporites</i> sp. A	58	3.6	Pteridophyta (Anemiaceae)
<i>Cicatricosisporites hallei</i> Delcourt & Sprumont 1955	55	3.4	Pteridophyta (Anemiaceae)
<i>Cicatricosisporites venustus</i> Deák 1963	32	2.0	Pteridophyta (Anemiaceae)
<i>Cicatricosisporites</i> spp.	57	3.5	Pteridophyta (Anemiaceae)
<i>Concavissimisporites informis</i> Döring 1965	34	2.1	Pteridophyta (Cyatheaceae/Dicksoniaceae)
<i>Costatoperforosporites triangulatus</i> Deák 1962	10	0.6	Pteridophyta (Anemiaceae)
<i>Costatoperforosporites</i> sp.	34	2.1	Pteridophyta (Anemiaceae)
<i>Crybelosporites pannuceus</i> (Brenner 1963) Srivastava 1977	27	1.7	Pteridophyta (Marsileaceae)
<i>Cyathidites australis</i> Couper 1953	48	2.9	Pteridophyta (Cyatheaceae/Dicksoniaceae or Lygodiaceae)
<i>Cyathidites punctatus</i> (Delcourt & Sprumont) Delcourt, Dettmann & Hughes 1963	43	2.6	Pteridophyta (Cyatheaceae/Dicksoniaceae or Lygodiaceae)
<i>Cibotiumspora juncta</i> (Kara-Murza, 1956) Zhang 1978	9	0.6	Pteridophyta (Gleicheniaceae or Matoniaceae)
<i>Densoisporites velatus</i> Weyland & Krieger 1953 emend. Dettmann 1963	15	0.9	Lycophyta (Selaginellaceae)
<i>Gregussisporites orientalis</i> Juhász & Smirnova 1985	12	0.7	Pteridophyta
<i>Ischyosporites pseudoreticulatus</i> (Couper, 1958) Döring 1965	22	1.3	Pteridophyta (Lygodiaceae)
<i>Ischyosporites punctatus</i> Cookson & Dettmann 1958	39	2.4	Pteridophyta (Lygodiaceae)
<i>Laevigatosporites ovatus</i> Wilson & Webster 1946	23	1.4	Pteridophyta (Polypodiaceae)
<i>Patellasporites tavadensis</i> Groot & Groot 1962	31	1.9	Pteridophyta
<i>Patellasporites</i> sp.	14	0.9	Pteridophyta
<i>Plicatella</i> sp.	23	1.4	Pteridophyta (Schizaeaceae)
<i>Taurosporites segmentatus</i> Stover 1962	11	0.7	Bryophyta (Hepaticae)
<i>Todisporites major</i> Couper 1958	17	1.0	Pteridophyta (?Osmundaceae)
<i>Todisporites minor</i> Couper 1958	20	1.2	Pteridophyta (?Osmundaceae)
<i>Triporetetes reticulatus</i> (Pocock, 1962) Playford 1971	19	1.2	Bryophyta (Hepaticae)
Pollen grains (Gymnosperms)			
<i>Alisporites rotundus</i> Rouse 1959	6	0.4	?Pteridospermales
<i>Araucariacites australis</i> Cookson 1947	93	5.7	Coniferophyta (Araucariaceae)
<i>Araucariacites</i> sp.	34	2.1	Coniferophyta (Araucariaceae)
<i>Balmeiopsis limbata</i> (Balme, 1957) Archangelsky 1979	7	0.4	Coniferophyta (Araucariaceae)
<i>Callialasporites dampieri</i> (Balme, 1957) Dev 1961 emend. Norris 1969	22	1.3	Coniferophyta (Araucariaceae)
<i>Callialasporites</i> sp.	14	0.9	Coniferophyta (Araucariaceae)
<i>Cedripites</i> sp.	5	0.3	Coniferophyta (Pinaceae)
<i>Cerebropollenites mesozoicus</i> (Couper, 1958) Nilsson 1958	32	2.0	?Coniferophyta
<i>Classopollis torosus</i> Burger 1965	88	5.4	Coniferophyta (Cheirolepidiaceae)
<i>Classopollis</i> spp.	140	8.6	Coniferophyta (Cheirolepidiaceae)
<i>Cycadopites follicularis</i> Wilson & Webster 1946	29	1.8	Cycadales or Bennettiales
<i>Cycadopites</i> sp.	48	2.9	Cycadales or Bennettiales
<i>Eucommiidites minor</i> Groot & Penny 1960	15	0.9	Erdtmanithecales
<i>Eucommiidites</i> sp.	23	1.4	Erdtmanithecales
<i>Ephedripites</i> sp.	6	0.4	Gnetales
<i>Monosulcites minimus</i> Cookson 1947	21	1.3	Bennettiales
<i>Pinuspollenites</i> sp.	10	0.6	Coniferophyta (Pinaceae)
<i>Piceapollenites</i> sp.	13	0.8	Coniferophyta (Pinaceae)
<i>Spheripollenites psilatus</i> Couper 1958	66	4.0	Coniferophyta (Cupressaceae)
Undetermined bisaccate pollen grains	112	6.9	unknown Coniferophyta
Pollen grains (Angiosperms)			
<i>Afropollis</i> sp.	3	0.2	?Angiospermae
<i>Clavatipollenites hughesii</i> Couper 1958	15	0.9	Angiospermae (Chloranthaceae)
Monosulcate pollen grains	2	0.1	Angiospermae
<i>Stellatopollis barghoornii</i> Doyle 1975	8	0.5	Angiospermae
<i>Senectotetradites</i> sp. (obligate tetrads)	7	0.4	Angiospermae (Eudicotyledoneae)
Total	1632	100.0	

For stratigraphic purposes, the most useful comparisons of the Carregueira palynoflora are with sequences in Portugal, England, and the Atlantic and Gulf Coastal Plains of the USA, which were also located in the Southern Laurasia province. Within this province, differences in stratigraphic ranges due to climatic and migrational

factors, of the sort seen between Southern Laurasia and Northern Gondwana, are presumably less important. Several sequences are long and closely sampled enough for some confidence in the validity of observed temporal changes through the Aptian–Albian; others represent shorter intervals but provide well-dated reference points.

The most informative Portuguese pollen sequences (Heimhofer et al., 2005, 2007) are from two long coastal sections, which consist of nearshore marine deposits that are dated primarily by dinoflagellates. The Luz section in the Algarve Basin (southwest Portugal) is thought to be nearly continuous through the Aptian and lower Albian. The Cresmina section in the Lusitanian Basin (central Portugal, ca. 120 km SW of Carregueira) extends from the upper Barremian to the middle Albian but is interrupted by a major hiatus comprising much of the Aptian, which corresponds to the regional unconformity at the base of the Figueira da Foz Formation. Less intensively sampled but well-dated marine deposits in England provide important corroborative evidence (Kemp, 1968, 1970; Laing, 1975).

In the Aptian at the Luz section, the only angiosperm pollen types are diverse columellar monosulcates. Tricolpate pollen with reticulate sculpture appears ca. 11 m above the base of the lower Albian as inferred from the first occurrence of the dinoflagellate *Dinopterygium cladoides* Deflandre. At Cresmina, reticulate tricolpates occur in the first samples above the unconformity, ca. 7 m below *Dinopterygium cladoides*. Assuming *Dinopterygium cladoides* is reliable as an Albian index fossil, these data indicate that the first tricolpates at Luz are lower Albian, but those at the Cresmina section could be either lower Albian or upper Aptian. In both sections, reticulate monosulcates with thickened sulcus margins (*Retimonocolpites* sp. 7) appear at approximately the same level. Similar pollen, described by Kemp (1968) as *Clavatipollenites rotundus*, co-occurs with the first reticulate tricolpates in the lowermost Albian of England (Kemp, 1968; Laing, 1975). Higher in the lower Albian in both Portuguese sections, reticulate tricolpates are joined by tricolpates with striate sculpture (*Striatopollis* spp.) and permanent tetrads of tricolpate grains, as well as additional monosulcate taxa.

Because of the low diversity of angiosperms at Carregueira, they provide limited evidence for correlation with the Portuguese marine sections. Small monosulcates of the *Clavatipollenites hughesii* type range throughout the Barremian–middle Albian, as in England (Kemp, 1968; Hughes, 1994) and Scandinavia (Vajda, 2001). Heimhofer et al. (2007) reported *Stellatopollis barghoornii* from the upper Aptian at Luz and the lower Albian at Cresmina, and other *Stellatopollis* species from the lower Aptian to the middle Albian. *Stellatopollis*, including forms close to *Stellatopollis barghoornii*, extends back to the Barremian in the Wealden (Hughes et al., 1979; Hughes, 1994), Gabon and Congo (Doyle et al., 1977; Doyle, 1992), and Egypt (Ibrahim, 2002). Heimhofer et al. (2007) did not include *Afropollis* in their occurrence charts because they did not consider it angiospermous, but they noted that it had “rare, but consistent occurrences”. Although *Afropollis* is most common in Northern Gondwana, where it ranges from upper Barremian to lower Cenomanian (Doyle et al., 1982; Gübeli et al., 1984; Penny, 1989; Regali and Viana, 1989; Doyle, 1992), it also occurs in the upper Barremian of the Scotian Shelf, Canada (pers. comm. from F. Stone cited in Doyle et al., 1982) and the Wealden (Penny, 1989).

We observed no single tricolpate grains in the Carregueira samples, although tricolpate pollen with reticulate, foveolate, and striate sculpture occurs *in situ* in mesofossils from other localities in the Famacão Member of the Figueira da Foz Formation (von Balthazar et al., 2005; Pedersen et al., 2007; Friis et al., 2011; Mendes et al., 2014b). However, the tetrads identified as *Senectotetradites* sp. are made up of reticulate tricolpate monads. Heimhofer et al. (2007) reported that tricolpate tetrads of *Virgo* cf. *amiantopollis* and aff. *Artiopollis* cf. *praecox* appear in the upper part of the lower Albian, but these species differ from the Carregueira tetrads: both have finer sculpture, while *Virgo* differs further in having poroid apertures.

In Delaware, Maryland, and Virginia, USA, Cretaceous deposition at the outcrop area began with the fluvial-deltaic deposits of the

Potomac Group. The palynological sequence is based on cores from several wells in Maryland (Brenner, 1963) and Delaware (Brenner 1967; Doyle and Robbins, 1977), plus numerous outcrop samples (Brenner, 1963; Doyle, 1969, 1992; Wolfe and Pakiser, 1971; Doyle and Hickey 1976; Hickey and Doyle, 1977; Upchurch and Doyle, 1981). Because these deposits are almost entirely continental, they are dated mainly by palynological correlations with marine sequences elsewhere in Southern Laurasia.

Brenner (1963) proposed two informal palynozones in the Potomac, Zone I and Zone II, with the latter divided into Subzones II-A and II-B. This zonation was extended upward and refined by Doyle and Robbins (1977). Brenner (1963) first observed tricolpates at the base of Zone II, along with several index species of spores. However, Doyle and Hickey (1976) and Doyle and Robbins (1977) extended reticulate tricolpates down into upper Zone I (Arundel Clay and equivalents), along with monosulcates of the *Clavatipollenites rotundus* type (as aff. *Retimonocolpites dividuus*). Ideas on the age of the Zone I-II boundary have varied. Brenner (1963) suggested that it corresponded to a hiatus between the Aptian and Albian, but Doyle and Hickey (1976) and Doyle and Robbins (1977) argued that upper Zone I was lowest Albian, based on the lower Albian appearance of reticulate tricolpates and *Clavatipollenites rotundus* in England (Kemp, 1968; Laing, 1975), while Doyle (1992) placed the boundary some way down in the Aptian. However, in a comparison of the Potomac and Portuguese sections, Hochuli et al. (2006) inferred a major hiatus between Zones I and II, and they considered upper Zone I lower Albian, based on the reticulate tricolpates. They dated lower Zone II as middle or even upper Albian, but a middle Albian age is favoured by correlations of middle Subzone II-B with a well-dated middle Albian flora in Oklahoma (Hedlund and Norris, 1968; Doyle and Robbins, 1977; Massoni et al., 2015; Tanrikulu et al., 2018). Finally, Tanrikulu et al. (2018) correlated a well-dated upper lower Albian palynoflora from the Glen Rose Formation of Texas with the upper lower Albian of Portugal and the missing interval between Zones I and II, based on the presence of both reticulate and striate tricolpates and *Clavatipollenites rotundus*.

Angiosperm pollen does not help much in correlating the Carregueira palynoflora with the Potomac sequence. Pollen of the *Clavatipollenites hughesii* type ranges throughout the Potomac, while *Afropollis* is exceedingly rare (Doyle et al., 1982; Doyle, 1992). Doyle and Robbins (1977) first recorded aff. *Stellatopollis barghoornii* in lower Subzone II-B, presumably middle Albian, but other species of *Stellatopollis* occur in lower Zone I (Doyle et al., 1975; Doyle and Hickey, 1976; Doyle, 1992). Tricolpate tetrads comparable to *Senectotetradites* are not known from the Potomac, but tetrads of the *Virgo* type, identified as *Ajatipollis*, appear in lower Subzone II-B (Doyle and Robbins, 1977).

Better evidence for correlation of the Carregueira flora with the Potomac Group, the Glen Rose, and the English section of Kemp (1970) comes from the spores (spores from the Portuguese coastal sections have not been described in detail). These include Zone II index spores of Brenner (1963), which appear at or near the base of Zone II. Given the evidence for a hiatus between Zones I and II, these could have appeared in the Potomac area at any time in the missing interval between the two zones, either before or after the time of the Glen Rose palynoflora. Most diagnostic are *Apiculatisporis babsae* (Fig. 4F), first observed by Kemp (1970) in the middle Albian of England, and *Crybelosporites pannuceus* (Fig. 4J, K). According to Singh (1971), *Camazonosporites insignis* (Fig. 5A, B) is the same as *Lycopodiacidites cerniidites* of Brenner (1963), which Brenner found only in Subzone II-B; however, Kemp (1970) reported *Camazonosporites insignis* from the mid-Aptian through the Albian of England. *Cicatricosisporites* sp. A appears to be identical to a Glen Rose spore identified by Tanrikulu et al. (2018, pl. 1,

fig. 10) as *Cicatricosisporites* sp., which does not correspond closely to any spore reported from the Potomac. These considerations indirectly support the view that the Carregueira horizon correlates with the missing interval between Potomac Zones I and II and with the upper lower Albian of Texas.

5.2. Composition of the vegetation and environmental considerations

The succession at the Carregueira site was deposited in a typical non-marine fluvial environment, with episodes of low-energy overbank sedimentation evidenced both by the sedimentology and the palynology.

The palynofloral assemblages show a predominance of hygrophilous taxa, mainly ferns. The occurrence of fresh-water algae assigned to Zygnemataceae, the colonial alga *Schizosporis reticulatus*, spores of the aquatic fern family Marsileaceae (*Crybelosporites pannuceus*), and seeds possibly related to Nymphaeales indicates freshwater conditions in small lakes, ponds or other water bodies on the fluvial floodplain (van Geel and Grenfell, 1996; Worobiec, 2014; Vajda et al., 2020). The abundance of spores ascribed to Anemiaceae, Cyatheaceae/Dicksoniaceae and Osmundaceae indicates the presence of a diverse community of ferns. Extant members of these families inhabit a wide range of environments, including stream and pond margins and forest understorey vegetation. The presence of bryophytes may indicate wet and enriched soil conditions on the forest floor.

The conifer element provides insights on the broader regional climate. *Classopollis*, the most abundant conifer pollen (14%), represents Cheirolepidiaceae, which are notable for their xeromorphic vegetative morphology and have long been considered indicators of hot and dry climates (Vakhrameev, 1970, 1981); with some exceptions (e.g., Tosolini et al., 2015), they are rare or absent at high palaeolatitudes. However, the frequency of *Classopollis* at Carregueira is comparable to that in the Potomac Group (average 16%; Brenner, 1963), and much lower than in the salt-bearing South Atlantic rift basins of Gabon, Congo, and Brazil, south of the palaeoequator, which appear to represent the most arid areas within the Southern Gondwana province (Brenner, 1976; Doyle et al., 1982; Carvalho et al., 2016). Areas of Southern Gondwana near the palaeoequator, such as Israel, Egypt, and Peru (Doyle et al., 1982; Schrank, 1983; Brenner, 1996; Carvalho et al., 2016; Mejía-Velasquez et al., 2018), have lower *Classopollis* frequencies (e.g., <11% in Egypt, <25% in Peru; Schrank, 1983; Mejía-Velasquez et al., 2018) and more ferns and Araucariaceae, suggesting they represent a wetter equatorial belt. However, *Classopollis* frequencies also vary with local environment, reaching 78% in marine-influenced facies in the Potomac Group and the lagoonal Glen Rose Formation of Texas (Upchurch and Doyle, 1981; Tanrikulu et al., 2018).

These observations suggest that the climate in central Portugal was similar to that of the Potomac area but wetter than that of the South Atlantic rift basins. It may have been comparable in humidity to wetter areas in Northern Gondwana but cooler, judging from the presence of bisaccate conifers. This picture is consistent with the clay mineralogy, which points to intense weathering under warm and wet conditions, as earlier inferred from coeval deposits of the western margin of Iberia based on mudstone geochemistry and mineralogy (Rocha and Gomes, 1995; Dinis et al., 2016). This evidence for a moderately humid climate in central Iberia contrasts with evidence for substantially drier conditions in southern Iberia (Heimhofer et al., 2012; Dinis et al., 2020). The dominance of angiosperm remains in the mesofossil flora, including delicate floral structures, indicates a relatively short transport distance and therefore implies that angiosperms grew within the lowland basin of deposition under wet conditions.

5.3. Comparison with palynofloras of other Aptian–Albian mesofossil localities

Informative palynofloras have been reported from other Lower Cretaceous mesofossil localities in the Lusitanian Basin. Studies of these palynofloras have mainly focused on taxonomic composition and its palaeoecological significance (Mendes et al., 2011, 2014a, 2017, 2018; Mendes and Friis, 2018).

The palynofloral assemblage from the Carregueira site shows similarities in general composition to other palynofloras from the lower part of the Figueira da Foz Formation in the Juncal region, at Chicalhão (Mendes et al., 2014a) and Nossa Senhora da Luz (Mendes and Friis, 2018), suggesting that they are probably more or less contemporaneous. Furthermore, in all three floras, fern spores and conifer pollen grains dominate the palynological assemblages quantitatively as well as qualitatively, while angiosperm pollen grains are subordinate. The most abundant fern spores at Chicalhão and Nossa Senhora da Luz are assignable to Anemiaceae and Cyatheaceae/Dicksoniaceae, elements of ground cover and tree ferns growing under humid conditions in riparian communities. Interestingly no macrofossil or mesofossil remains of ferns have been documented from any of the three localities.

As in the Carregueira palynoflora, the most prominent component in the Chicalhão and Nossa Senhora da Luz conifer assemblages is *Classopollis*. Because Cheirolepidiaceae and other conifers recognized in the three palynofloras were presumably wind-pollinated, their pollen may have been transported to the deposition basin from drier habitats. The Carregueira palynoflora does differ from the other two in the presence of fresh-water algae, such as *Ovoidites parvus*, *Ovoidites spriggii* and *Schizosporis reticulatus*. Reticulate monosulcates and *Senectotetradites* occur in all three floras, while Chicalhão has one reticulate tricolpate species. It is noteworthy that both the Carregueira and the Nossa Senhora da Luz palynofloras include *Stellatopollis barghoornii* and the primarily Gondwanan genus *Afropollis*, highlighting the possibility that Iberia served as a “bridge” between Northern Gondwanan and Southern Laurasia during the Early Cretaceous (see also Batten and Li (1987); Hergreen and Dueñas Jiménez (1990).

As noted in earlier studies (Mendes et al., 2014a; Mendes and Friis, 2018), these and other Portuguese mesofossil floras show a combination of abundant and diverse angiosperm mesofossils with rare and low-diversity dispersed angiosperm pollen. Often many more pollen types are known *in situ* in stamens or on stigmas of mesofossils than in the dispersed palynoflora from the same deposits. Considering taxa in the mesofossil flora (see Material and methods), *Canrightiopsis* has pollen of the *Clavatipollenites* type (Friis et al., 2017), which occurs in the palynoflora (Fig. 6J), but *Anacostia* has pollen of the *Similipollis* type (Friis et al., 1997), which we have not observed. This contrast in abundance and diversity of angiosperms in the pollen and mesofossil records is not a universal feature of Aptian–Albian floras; in the Potomac Group, the upper Albian West Brothers mesofossil flora (Friis et al., 1988; Drinnan et al., 1991) is associated with unusually abundant and diverse angiosperm pollen, including several taxa illustrated by Doyle (1969, fig. 2).

A factor that might be involved is sedimentary size sorting: larger mesofossils might have settled out at the site of deposition while pollen remained suspended and was transported further. This could also mean that spores are better represented than angiosperm pollen, which is generally much smaller. However, the poor sorting of the deposits suggests that this explanation may not be sufficient. The greater diversity of *in situ* angiosperm pollen relative to dispersed pollen may reflect the role of mesofossils in “concentrating” pollen that was attenuated in the dispersed record because the parent plants were subordinate or insect pollinated. In

either case, more intensive scanning of slides might reveal pollen types previously only known *in situ* in mesofossils.

A different sort of contrast is illustrated by *Stellatopollis* and *Senectotetradites*, which are seen in the palynofloras but have not been associated with mesofossils. This could be because their parent plants were growing farther from the site of deposition, or because their flowers had particularly low fossilization potential.

6. Conclusions

A rich and well-preserved palynoflora from the Famalicão Member of the Figueira da Foz Formation at the Carregueira locality in west-central Portugal provides new data on the vegetation and climate during the Early Cretaceous in this region. Palynological analysis reveals a typical Early Cretaceous palynoflora dominated by gymnosperm pollen and fern spores, many of which are assignable to Anemiaceae (Schizaeales), Cyatheaceae/Dicksoniaceae (Cyatheales) and Osmundaceae.

The association of abundant spores and pollen of both the xerophytic extinct conifer family Cheirolepidiaceae (*Classopollis*) and other conifers, particularly Araucariaceae and Pinaceae (bisaccate pollen), reflects the presence of wet fluvial habitats in the lowlands and drier but still moderately humid inland vegetation dominated by conifers. Angiosperms are poorly represented in the pollen assemblages but dominate the mesofossil flora, which also includes conifer seeds and numerous fragments of cheirolepidiaceae twigs.

Comparisons with palynofloras from well-dated nearshore marine sequences in Portugal, England, and Texas suggest correlation with the lower Albian, corresponding to a hiatus between Zones I and II of the Potomac Group in the eastern USA. The palynoflora also includes *Afropollis* and *Stellatopollis barghoornii*, which are more characteristic of Northern Gondwana, highlighting the possible role of Iberia as a “bridge” between the Southern Laurasian and Northern Gondwanan floral provinces during the Early Cretaceous.

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References

Batten, D.J., Li, W.B., 1987. Aspects of palynomorph distribution, floral provinces and climate during the Cretaceous. *Geologisches Jahrbuch, Reihe A* 96, 219–237.

Berthou, P.-Y., 1984. Albian–Turonian stage boundaries and subdivisions in the Western Portuguese Basin, with special emphasis on the Cenomanian–Turonian boundary in the Ammonite Facies and Rudist Facies. *Bulletin of the Geological Society of Denmark* 33, 41–45.

Berthou, P.-Y., Leereveld, H., 1990. Stratigraphic implications of palynological studies on Berriasian to Albian deposits from western and southern Portugal. *Review of Palaeobotany and Palynology* 66, 313–344.

Brenner, G.J., 1963. The spores and pollen of the Potomac Group of Maryland, vol. 27. Maryland Department of Geology, Mines and Water Resources Bulletin, pp. 1–215.

Brenner, G.J., 1967. Early angiosperm pollen differentiation in the Albian to Cenomanian deposits of Delaware (U.S.A.). *Review of Palaeobotany and Palynology* 1, 219–227.

Brenner, G.J., 1976. Middle Cretaceous floral provinces and early migrations of angiosperms. In: Beck, C.B. (Ed.), *Origin and early evolution of angiosperms*. Columbia University Press, New York, pp. 23–47.

Brenner, G.J., 1996. Evidence for the earliest stage of angiosperm pollen evolution: a paleoquatorial section from Israel. In: Taylor, D.W., Hickey, L.J. (Eds.), *Flowering plant origin, evolution & phylogeny*. Chapman & Hall, New York, pp. 91–115.

Callapez, P., 1998. Estratigrafia e paleobiologia do Cenomaniano-Turoniano. O significado do eixo da Nazaré-Leiria-Pombal (Unpubl. PhD thesis). Universidade de Coimbra, Portugal.

Carvalho, M.A., Bengtson, P., Lana, C.C., 2016. Late Aptian (Cretaceous) paleoceanography of the South Atlantic Ocean inferred from dinocyst communities of the Sergipe Basin, Brazil. *Paleoceanography* 31, 2–26.

Chamley, H., 1989. *Clay mineralogy*. Springer, Berlin, p. 631.

Cunha, P.P., 1992. Estratigrafia e sedimentologia dos depósitos do Cretácico Superior e Terciário de Portugal Central, a leste de Coimbra (Unpubl. PhD thesis). Universidade de Coimbra, Portugal.

Cunha, P.P., Pena dos Reis, R., 1995. Cretaceous sedimentary and tectonic evolution of the northern sector of the Lusitanian Basin. *Cretaceous Research* 16, 155–170.

Dinis, J.L., Rey, J., de Graciansky, P.C., 2002. Le Bassin Lusitanien (Portugal) à l'Aptien supérieur–Albien: organisation séquentielle, proposition de corrélations, évolution. *Comptes Rendus Geoscience* 334, 757–764.

Dinis, J., Rey, J., Cunha, P.P., Callapez, P., Pena dos Reis, R., 2008. Stratigraphy and allogenic controls of the western Portugal Cretaceous: an updated synthesis. *Cretaceous Research* 29, 772–780.

Dinis, P.A., Dinis, J.L., Mendes, M.M., Rey, J., Pais, J., 2016. Geochemistry and mineralogy of the Lower Cretaceous of the Lusitanian Basin (western Portugal): deciphering palaeoclimates from weathering indices and integrated vegetational data. *Comptes Rendus Geoscience* 348, 139–149.

Dinis, P.A., Carvalho, J., Callapez, P.M., Mendes, M.M., Santos, V.F., Fernandes, P., 2020. Composition of Lower Cretaceous mudstones of the Algarve Basin and implications for Iberian palaeoclimates. *Cretaceous Research* 110. Article 104404.

Doyle, J.A., 1969. Cretaceous angiosperm pollen of the Atlantic Coastal Plain and its evolutionary significance. *Journal of the Arnold Arboretum* 50, 1–35.

Doyle, J.A., 1992. Revised palynological correlations of the lower Potomac Group (USA) and the Cocobeach sequence of Gabon (Barremian–Aptian). *Cretaceous Research* 13, 337–349.

Doyle, J.A., Endress, P.K., 2010. Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: Magnoliidae and eudicots. *Journal of Systematics and Evolution* 48, 1–35.

Doyle, J.A., Endress, P.K., 2014. Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: ANITA lines and relatives of Chloranthaceae. *International Journal of Plant Sciences* 175, 555–600.

Doyle, J.A., Endress, P.K., 2018. Phylogenetic analyses of Cretaceous fossils related to Chloranthaceae and their evolutionary implications. *The Botanical Review* 84, 156–202.

Doyle, J.A., Hickey, L.J., 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. In: Beck, C.B. (Ed.), *Origin and early evolution of angiosperms*. Columbia University Press, New York, pp. 139–206.

Doyle, J.A., Robbins, E.L., 1977. Angiosperm pollen zonation of the continental Cretaceous of the Atlantic Coastal Plain and its application to deep wells in the Salisbury Embayment. *Palynology* 1, 43–78.

Doyle, J.A., van Campo, M., Lugardon, B., 1975. Observations on exine structure of *Eucommiidites* and Lower Cretaceous angiosperm pollen. *Pollen et Spores* 17, 429–486.

Doyle, J.A., Biens, P., Doerenkamp, A., Jardiné, S., 1977. Angiosperm pollen from the pre-Albian Cretaceous of Equatorial Africa. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* 1, 451–473.

Doyle, J.A., Jardiné, S., Doerenkamp, A., 1982. *Afropollis*, a new genus of early angiosperm pollen, with notes on the Cretaceous palynostratigraphy and paleoenvironments of Northern Gondwana. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* 6, 39–117.

Drinnan, A.N., Crane, P.R., Friis, E.M., Pedersen, K.R., 1991. Angiosperm flowers and tricolpate pollen of buxaceous affinity from the Potomac Group (mid-Cretaceous) of eastern North America. *American Journal of Botany* 78, 153–176.

França, J.C., Zbyszewski, G., 1963. Carta Geológica de Portugal na escala 1:50 000. Notícia explicativa da folha 26-B (Alcobaça). Serviços Geológicos de Portugal, Lisboa.

Friis, E.M., Crane, P.R., Pedersen, K.R., 1988. Reproductive structures of Cretaceous Platanaceae. *Biologiske Skrifter Danske Videnskabernes Selskab* 31, 1–55.

Friis, E.M., Crane, P.R., Pedersen, K.R., 1997. *Anacostia*, a new basal angiosperm from the Early Cretaceous of North America and Portugal with trichotomocolpate/monocolpate pollen. *Grana* 36, 225–244.

Friis, E.M., Pedersen, K.R., Crane, P.R., 1999. Early angiosperm diversification: the diversity of pollen associated with angiosperm reproductive structures in Early Cretaceous floras from Portugal. *Annals of the Missouri Botanical Garden* 86, 259–296.

Friis, E.M., Pedersen, K.R., Crane, P.R., 2000. Reproductive structure and organization of basal angiosperms from the Early Cretaceous (Barremian or Aptian) of western Portugal. *International Journal of Plant Sciences* 161 (6 Suppl. 1), S169–S182.

Friis, E.M., Pedersen, K.R., Crane, P.R., 2006. Cretaceous angiosperm flowers: innovation and evolution in plant reproduction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232, 251–293.

- Friis, E.M., Pedersen, K.R., von Balthazar, M., Grimm, G.W., Crane, P.R., 2009. *Montianthus mirus* gen. et sp. nov., a nymphaealean flower from the Early Cretaceous of Portugal. *International Journal of Plant Sciences* 170, 1086–1101.
- Friis, E.M., Pedersen, K.R., Crane, P.R., 2010. Cretaceous diversification of angiosperms in the western part of the Iberian Peninsula. *Review of Palaeobotany and Palynology* 162, 341–361.
- Friis, E.M., Crane, P.R., Pedersen, K.R., 2011. Early flowers and angiosperm evolution. Cambridge University Press, Cambridge, p. 585.
- Friis, E.M., Grimm, G.W., Mendes, M.M., Pedersen, K.R., 2015. *Canrightiopsis*, a new Early Cretaceous fossil with *Clavatiipollenites*-type pollen bridge the gap between extinct *Canrightia* and extant Chloranthaceae. *Grana* 54, 184–212.
- Friis, E.M., Crane, P.R., Pedersen, K.R., 2017. *Saportanthus*, an extinct genus of Laurales from the Early Cretaceous of Portugal. *International Journal of Plant Sciences* 78, 650–672.
- Friis, E.M., Crane, P.R., Pedersen, K.R., 2018. Extinct taxa of exotestal seeds close to Austrobaileyales and Nymphaeales from the Early Cretaceous of Portugal. *Fossil Imprint* 74, 135–158.
- Friis, E.M., Crane, P.R., Pedersen, K.R., 2019. The Early Cretaceous mesofossil flora of Torres Vedras (NE of Forte da Forca), Portugal: a palaeofloristic analysis of an early angiosperm community. *Fossil Imprint* 75, 153–257.
- Groot, J.G., Groot, C.R., 1962. Plant microfossils from Aptian, Albian and Cenomanian deposits of Portugal. *Comunicacoes dos Servicos Geologicos de Portugal* 46, 133–176.
- Gübeli, A.A., Hochuli, P.A., Wildi, W., 1984. Lower Cretaceous turbiditic sediments from the Rif chain (northern Morocco) – palynology, stratigraphy and palaeogeographic setting. *Geologische Rundschau* 73, 1081–1114.
- Hasenboehler, B., 1981. Étude paléobotanique et palynologique de l'Albien et du Cénomaniens du "Bassin Occidental Portugais" au sud de l'accident de Nazaré (Province d'Estremadura, Portugal) (Unpubl. PhD thesis). Université Pierre et Marie Curie, Paris, France.
- Hedlund, R.W., Norris, G., 1968. Spores and pollen grains from Fredericksburgian (Albian) strata, Marshall County, Oklahoma. *Pollen et Spores* 10, 129–159.
- Heer, O., 1881. Contributions à la flore fossile du Portugal. Comissão dos Trabalhos Geológicos de Portugal, Lisboa, p. 51.
- Heimhofer, U., Hochuli, P.A., Burla, S., Dinis, J., Weissert, H., 2005. Timing of Early Cretaceous angiosperm diversification and possible links to major paleoenvironmental change. *Geology* 33, 141–144.
- Heimhofer, U., Hochuli, P.A., Burla, S., Weissert, H., 2007. New records of Early Cretaceous angiosperm pollen from Portuguese coastal deposits: implications for the timing of the early angiosperm radiation. *Review of Palaeobotany and Palynology* 144, 39–76.
- Heimhofer, U., Hochuli, P.A., Burla, S., Oberli, F., Adatte, T., Dinis, J.L., Weissert, H., 2012. Climate and vegetation history of western Portugal inferred from Albian near-shore deposits (Galé Formation, Lusitanian Basin). *Geological Magazine* 149, 1046–1064.
- Herngreen, G.F., Dueñas Jiménez, H., 1990. Dating of the Cretaceous Une Formation, Colombia and relationship with the Albian–Cenomanian African–South American microfloral province. *Review of Palaeobotany and Palynology* 66, 345–359.
- Hickey, L.J., Doyle, J.A., 1977. Early Cretaceous fossil evidence for angiosperm evolution. *The Botanical Review* 43, 1–104.
- Hochuli, P.A., Heimhofer, U., Weissert, H., 2006. Timing of early angiosperm radiation: recalibrating the classical succession. *Journal of the Geological Society, London* 163, 587–594.
- Horikx, M., Heimhofer, U., Dinis, J., Huck, S., 2014. Integrated stratigraphy of shallow marine Albian strata from the southern Lusitanian Basin of Portugal. *Newsletters on Stratigraphy* 47, 85–106.
- Horikx, M., Hochuli, P.A., Feist-Burkhardt, S., Heimhofer, U., 2016. Albian angiosperm pollen from shallow marine strata in the Lusitanian Basin, Portugal. *Review of Palaeobotany and Palynology* 228, 67–92.
- Horikx, M., Huck, S., Adatte, T., Heimhofer, U., 2017. Vegetation dynamics, angiosperm radiation and climatic changes in the Lusitanian Basin (Portugal) during Albian times. *Palaeogeography, Palaeoclimatology, Palaeoecology* 465, 30–41.
- Hughes, N.F., 1994. The enigma of angiosperm origins. Cambridge University Press, Cambridge, p. 303.
- Hughes, N.F., Drewry, G.E., Laing, J.F., 1979. Barremian earliest angiosperm pollen. *Palaeontology* 22, 513–535.
- Hundert, T., Piper, D.J.W., Pe-Piper, G., 2006. Genetic model and exploration guidelines for kaolin beneath unconformities in the Lower Cretaceous fluvial Chaswood Formation, Nova Scotia. *Exploration And Mining Geology* 15, 9–26.
- Ibrahim, M.I.A., 2002. New angiosperm pollen from the upper Barremian–Aptian of the Western Desert, Egypt. *Palynology* 26, 107–133.
- Kahle, M., Kleber, M., Jahn, R., 2002. Review of XRD-based quantitative analyses of clay minerals in soils: the suitability of mineral intensity factors. *Geoderma* 109, 191–205.
- Kemp, E.M., 1968. Probable angiosperm pollen from British Barremian to Albian strata. *Palaeontology* 11, 421–434.
- Kemp, E.M., 1970. Aptian and Albian miospores from southern England. *Palaeontographica Abteilung B* 131, 73–143.
- Laing, J.F., 1975. Mid-Cretaceous angiosperm pollen from southern England and northern France. *Palaeontology* 18, 775–808.
- Lidgard, S., Crane, P.R., 1988. Quantitative analyses of the early angiosperm radiation. *Nature* 331, 344–346.
- Massoni, J., Doyle, J., Sauquet, H., 2015. Fossil calibration of Magnoliidae, an ancient lineage of angiosperms. *Palaeontologia Electronica* 17 (3), 2FC, 25.
- Médus, J., 1982. Palynofloristic correlations of two Albian sections of Portugal. *Cuadernos de Geologia Iberica* 8, 781–809.
- Mejía-Velasquez, P.J., Manchester, S.R., Jaramillo, C.A., Quiroz, L., Fortini, L., 2018. Floristic and climatic reconstructions of two Lower Cretaceous successions from Peru. *Palynology* 42, 420–433.
- Mendes, M.M., Friis, E.M., 2018. The Nossa Senhora da Luz flora from the Early Cretaceous (early Aptian–late Albian) of Juncal in the western Portuguese Basin. *Acta Palaeobotanica* 58, 159–174.
- Mendes, M.M., Dinis, J., Pais, J., Friis, E.M., 2011. Early Cretaceous flora from Vale Painho (Lusitanian Basin, western Portugal): an integrated palynological and mesofossil study. *Review of Palaeobotany and Palynology* 166, 152–162.
- Mendes, M.M., Dinis, J., Pais, J., Friis, E.M., 2014a. Vegetational composition of the Early Cretaceous Chicalhão flora (Lusitanian Basin, western Portugal) based on palynological and mesofossil assemblages. *Review of Palaeobotany and Palynology* 200, 65–81.
- Mendes, M.M., Grimm, G.W., Pais, J., Friis, E.M., 2014b. Fossil *Kajanthus lusitanicus* gen. et sp. nov. from Portugal: floral evidence for Early Cretaceous Lardizabaceae (Ranunculales, basal eudicot). *Grana* 53, 283–301.
- Mendes, M.M., Barrón, E., Batten, D.J., Pais, J., 2017. A new species of the spore genus *Costatoperforosporites* from Early Cretaceous deposits in Portugal and its taxonomic and palaeoenvironmental significance. *Grana* 56, 401–409.
- Mendes, M.M., Barrón, E., Dinis, P., Rey, J., Batten, J.D., 2018. A new palynoflora from upper Barremian–lower Aptian rocks at Casal do Borracho, Torres Vedras, western Portugal, and its palaeoecological significance. *Cretaceous Research* 90, 363–374.
- Mendes, M.M., Polette, F., Cunha, P.P., Dinis, P., Batten, D.J., 2019. A new Hauterivian palynoflora from the Vale Cortiço site (central Portugal) and its palaeoecological implications for western Iberia. *Acta Palaeobotanica* 59, 215–228.
- Moore, D.M., Reynolds, R.C., 1997. X-ray diffraction and the identification and analysis of clay minerals. Oxford University Press, Oxford, p. 378.
- Oliveira, J.T., Pereira, E., Ramalho, M.M., Antunes, M.T., Monteiro, J.H., 1992. Carta Geológica de Portugal, escala 1:500.000. Serviços Geológicos de Portugal, Lisboa.
- Pais, J., Reyre, Y., 1981. Problèmes posés par la population sporo-pollinique d'un niveau à plantes de la série de Buarcos (Portugal). *Boletim da Sociedade Geologica de Portugal* 22, 35–40.
- Pedersen, K.R., von Balthazar, M., Crane, P.R., Friis, E.M., 2007. Early Cretaceous floral structures and *in situ* tricolpate-striate pollen: new early eudicots from Portugal. *Grana* 46, 176–196.
- Penny, J.H.J., 1986. An Early Cretaceous angiosperm pollen assemblage from Egypt. *Special Papers in Palaeontology* 35, 121–134.
- Penny, J.H.J., 1989. New Early Cretaceous forms of the angiosperm pollen genus *Afropollis* from England and Egypt. *Review of Palaeobotany and Palynology* 58, 289–299.
- Regali, M.S.P., Viana, C.F., 1989. Late Jurassic–Early Cretaceous in Brazilian sedimentary basins: correlation with the international standard scale. *Petrobras, Rio de Janeiro*, p. 95.
- Rey, J., 1972. Recherches géologiques sur le Crétacé inférieur de l'Estremadura (Portugal). *Memorias dos Servicos Geologicos de Portugal* 21, 1–477.
- Rey, J., 1993. Les unités lithostratigraphiques du Groupe de Torres Vedras (Estremadura, Portugal), vol. 79. *Comunicações do Instituto Geológico e Mineiro*, pp. 75–85.
- Rey, J., 2006. Stratigraphie séquentielle et séquences de dépôt dans le Crétacé inférieur du Bassin Lusitanien. *Ciencias da Terra* 6, 1–120. Volume Especial.
- Rey, J., de Graciansky, P.-C., Jacquín, T., 2003. Les séquences de dépôt dans le Crétacé inférieur du Bassin Lusitanien, vol. 90. *Comunicações do Instituto Geológico e Mineiro*, pp. 15–42.
- Rocha, F., Gomes, C., 1995. Palaeoenvironment of the Aveiro region of Portugal during the Cretaceous, based on clay mineralogy. *Cretaceous Research* 16, 187–194.
- Romariz, C., 1946. Estudo e revisão das formas portuguesas de *Frenelopsis*. *Boletim do Museu de Mineralogia e Geologia da Faculdade de Ciências da Universidade de Lisboa* 14, 135–149.
- Saporta, G., 1894. Flore fossile du Portugal. *Nouvelles contributions à la flore Mésozoïque, accompagnées d'une notice stratigraphique*. Direction des Travaux Géologiques du Portugal, Lisboa, p. 288.
- Schrank, E., 1983. Scanning electron and light microscopic investigations of angiosperm pollen from the Lower Cretaceous of Egypt. *Pollen et Spores* 25, 213–242.
- Schrank, E., 2010. Pollen and spores from the Tendaguru Beds, Upper Jurassic and Lower Cretaceous of southeast Tanzania: palynostratigraphical and palaeoecological implications. *Palynology* 34, 3–42.
- Singh, C., 1971. Lower Cretaceous microfloras of the Peace River area, northwestern Alberta. *Research Council of Alberta, Bulletin* 28, 1–310.
- Tanrikulu, S., Doyle, J.A., Delusina, I., 2018. Early Cretaceous (Albian) spores and pollen from the Glen Rose Formation of Texas and their significance for correlation of the Potomac Group. *Palynology* 42, 438–456.
- Teixeira, C., 1945. Nymphaeacées fossiles du Portugal. *Serviços Geológicos de Portugal, Lisboa*, p. 13.
- Teixeira, C., 1947. Nouvelles recherches et revision de la flore de Cercal. *Boteria, Série de Ciências Naturais* 16 (43), 5–14 fasc. 1.
- Teixeira, C., 1948. Flora mesozóica portuguesa, parte I. *Serviços Geológicos de Portugal, Lisboa*, p. 119.
- Teixeira, C., 1950. Flora mesozóica portuguesa, parte II. *Serviços Geológicos de Portugal, Lisboa*, p. 33.

- Teixeira, C., 1952. Notes sur quelques gisements des végétaux fossils du Crétacé des environs de Leiria. *Revista da Faculdade de Ciências de Lisboa* 2, 133–154.
- Tosolini, A.-M.P., McLoughlin, S., Wagstaff, B.E., Cantrill, D.J., Gallagher, S.J., 2015. Cheirolepidiacean foliage and pollen from Cretaceous high-latitudes of south-eastern Australia. *Gondwana Research* 27, 960–977.
- Traverse, A., 2007. *Paleopalynology*, second ed. Springer, Dordrecht, p. 813.
- Trincão, P., 1990. Esporos e pólenes do Cretácico inferior (Berriasiano-Aptiano) de Portugal: paleontologia e biostratigrafia (Unpubl. PhD thesis). Universidade Nova de Lisboa, Portugal.
- Upchurch Jr., G.R., Doyle, J.A., 1981. Paleoeology of the conifers *Frenelopsis* and *Pseudofrenelopsis* (Cheirolepidiaceae) from the Cretaceous Potomac Group of Maryland and Virginia. In: Romans, R.C. (Ed.), *Geobotany II*. Plenum, New York, pp. 167–202.
- Vajda, V., 2001. Aalenian to Cenomanian palynofloras of SW Scania, Sweden. *Acta Paleontologica Polonica* 46, 403–426.
- Vajda, V., McLoughlin, S., Mays, C., Frank, T.D., Fielding, C.R., Tevyaw, A., Lehsten, V., Bocking, M., Nicoll, R.S., 2020. End-Permian (252 Mya) deforestation, wildfires and flooding—An ancient biotic crisis with lessons for the present. *Earth and Planetary Science Letters* 529. Article 115875.
- Vakhrameev, V.A., 1970. Zakonomernosti rasprostraneniya i paleoekologiya mezo-zoyskikh khvoynnykh Cheirolepidiaceae. *Paleontologicheskii Zhurnal* 1970 19–34.
- Vakhrameev, V.A., 1981. Pollen *Classopollis*: indicator of Jurassic and Cretaceous climates. *Palaeobotanist* 28–29, 301–307.
- van Geel, B., Grenfell, H.R., 1996. Spores of Zygnemataceae (Chapter 7A). In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: principles and applications*, vol. 1. American Association of Stratigraphic Palynologists, pp. 173–179.
- Velde, B., 1995. *Origin and mineralogy of clays*. Springer, Berlin, p. 335.
- Villanueva-Amadoz, U., Sender, L.M., Diez, J.B., Ferrer, J., Pons, D., 2011. Palynological studies of the boundary marls unit (Albian–Cenomanian) from northeastern Spain. Paleophytogeographical implications. *Geodiversitas* 33, 137–176.
- von Balthazar, M., Pedersen, K.R., Friis, E.M., 2005. *Teixeiraea lusitanica* gen. et sp. nov., a ranunculalean flower from the Early Cretaceous of Portugal. *Plant Systematics and Evolution* 255, 55–75.
- Wilson, R.C.L., Hiscott, R.N., Willis, M.G., Gradstein, F.M., 1989. The Lusitanian basin of west-central Portugal: Mesozoic and Tertiary tectonic, stratigraphic, and subsidence history. In: Tankard, A.J., Balkwill, H. (Eds.), *Extensional tectonics and stratigraphy of the North Atlantic margins*, vol. 46. American Association of Petroleum Geologists, pp. 341–361.
- Wing, S.L., Boucher, L.D., 1998. Ecological aspects of the Cretaceous flowering plant radiation. *Annual Review of Earth and Planetary Sciences* 26, 379–421.
- Wolfe, J.A., Pakiser, H.M., 1971. Stratigraphic interpretations of some Cretaceous microfossil floras of the Middle Atlantic States. U.S. Geological Survey Professional Paper 750-B, B35–B47.
- Worobiec, E., 2014. Fossil zygospores of Zygnemataceae and other microremains of freshwater algae from two Miocene palaeosinkholes in the Opole region, SW Poland. *Acta Palaeobotanica* 54, 113–157.